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Two New Species of *Gargamella* (Mollusca, Nudibranchia) from South Africa

by

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This paper describes two new species of the genus *Gargamella* from South Africa. *Gargamella gravastella* is characterized by a dark grey notum with white-ringed dark spots, and a dense covering of caryophyllidia. Distinct reproductive features include a smooth accessory gland, and a series of large penial hooks, each having a wide base and short cusp. *Gargamella bovina* is characterized by a white notum covered with dark brown spots, and short caryophyllidia. Its outermost lateral tooth is notably smaller than the other outer lateral teeth. Distinct reproductive features include a large lobate accessory gland which bears a muscular attachment to the female gland, and a series of large penial hooks, each with a wide base and long cusp. Additional information on the caryophyllidia, reproductive, and radular characteristics is also provided.

In order to determine the systematic position of *G. gravastella* and *G. bovina*, a phylogenetic analysis has been carried out, including representatives of the genera *Baptodoris*, *Platydoris* and *Gargamella*. The phylogeny obtained supports the placement of these two new species in the genus *Gargamella*. In addition, *Gargamella*, *Platydoris* and *Baptodoris* appear to be distinct, monophyletic genera.

The genus *Gargamella* Bergh, 1894 presently contains only one valid species: *Gargamella immaculata* Bergh, 1894 from South America. Miller (1996) synonymized *Gargamella no-vozealandica* Eliot, 1907, from New Zealand, with *Jorunna pantherina* (Angas, 1864), and Schrödl (1997) regarded *Gargamella latior* Odhner, 1926, another nominal species described from South America, as a junior synonym of *G. immaculata*, based on observations of the internal anatomy and geographical range.

Gosliner (1983) reported two additional, undescribed species of *Gargamella* from South Africa, both distinguishable from the other described species. The present paper describes these two new species based on specimens deposited in the Department of Marine Biology of the South African Museum, Cape Town (SAM). Comparative material of other species discussed in this paper was obtained from the Department of Invertebrate Zoology of the California Academy of Sciences (CASIZ), the Department of Invertebrate Zoology of the Swedish Museum of Natural History (SMNHI) and the Museo Nacional de Ciencias Naturales of Madrid, Spain (MNCN).

SPECIES DESCRIPTIONS

Gargamella gravastella sp. nov.

Figs. 1A, 2, 3

Gargamella sp. 1 Gosliner, 1987:70, fig. 94.

TYPE MATERIAL. — HOLOTYPE: Dale Brook, False Bay, Cape Province, South Africa (34°07'26"S, 18°27'33"E), 18 September, 1982, 11 mm preserved length, collected by T. M. Gosliner (SAM A35382). PARATYPES: Dale Brook, False Bay, Cape Province, South Africa (34°07'26"S, 18°27'33"E), 18 September, 1982, one specimen 4 mm preserved length (SAM A54295); date unknown, one specimen 17 mm preserved length, dissected, collected by T. M. Gosliner (SAM A35384); 10 September 1982, one specimen 24 mm preserved length, dissected, collected by T. M. Gosliner (SAM A35383); 18 September, 1982, one specimen 10 mm preserved length, dissected, collected by T. M. Gosliner (SAM A35381).

ETYMOLOGY. — *Gargamella gravastella* is named for its external coloration and body texture. The word *gravastella* is Latin for "grey headed fellow" and makes reference to the rough grey notum of this caryophyllidia-bearing dorid nudibranch.

DISTRIBUTION. — Specimens of this species have been found only at Dale Brook, False Bay, Cape Peninsula, Cape Province, South Africa.

EXTERNAL MORPHOLOGY. — The living animal (Fig. 1A) has a dark gray notum marked with several dark gray spots, each surrounded by a white circle. The perfoliate rhinophores are pale yellowish white in color. They consist of 8 transverse lamellae. The gill is also pale yellowish white, the same color as the rhinophores, and is composed of 8 unipinnate branchial leaves. The anal papilla lies within, and closes the circlet of the branchial leaves.

The body shape is oval with a slightly undulate mantle. The body is covered with many short caryophyllidia tubercles measuring about 70 μ m. Each caryophyllidium consists of a rounded central ciliated tubercle that occupies completely the space inside the surrounding ring of spicules. Several (5–9) tall spicules project around the tubercle margin (Fig. 2D). The foot is bilabiate and notched. (Fig. 3B) The foot is wide in relation to the mantle margin. The oral tentacles are well formed, and appear conical in shape.

BUCCAL ARMATURE. — The jaws are smooth, with no rodlets. The radular formulae of two specimens examined are $31 \times 39.0.39$ (SAM A35383) and $36 \times 42.0.42$ (SAM A35384). The inner lateral teeth (Fig. 2A) are smooth, and gradually increase in size toward the mid-lateral teeth (Fig. 2B), which also lack denticles. The outer lateral teeth (Fig. 2C) are smooth as well, and gradually decrease in size. The outermost lateral teeth are not extremely small relative to the other outer lateral teeth.

REPRODUCTIVE SYSTEM. — The ampulla is tubular and simple. It narrows before branching into the short oviduct, which enters the female gland, and the large prostate (Fig. 2A). The prostate is nearly as wide as the female gland mass in the specimens examined. At the proximal end of the prostate, there is a junction at which the long, convoluted deferent duct narrows and becomes the tubular ejaculatory duct. The penial bulb widens at its proximal end, and is armed with four rows of hooks. The hooks have a wide base approximately 0.1 mm wide, and a relatively short cusp approximately 25 μ m long (Fig. 2C). The deferent duct and vaginal duct meet, forming an atrium where there is a small spherical accessory gland, which lacks any armature. The proximal end of the vaginal duct is very wide, wider than the deferent duct. The vagina narrows at the distal end before entering the oval shaped bursa copulatrix. Another duct leads from the bursa copulatrix to the oval shaped, stalked seminal receptacle. This duct, which is located directly adjacent to the junction of the vaginal duct and bursa copulatrix, is the same width as the narrowest part of the vaginal duct and is

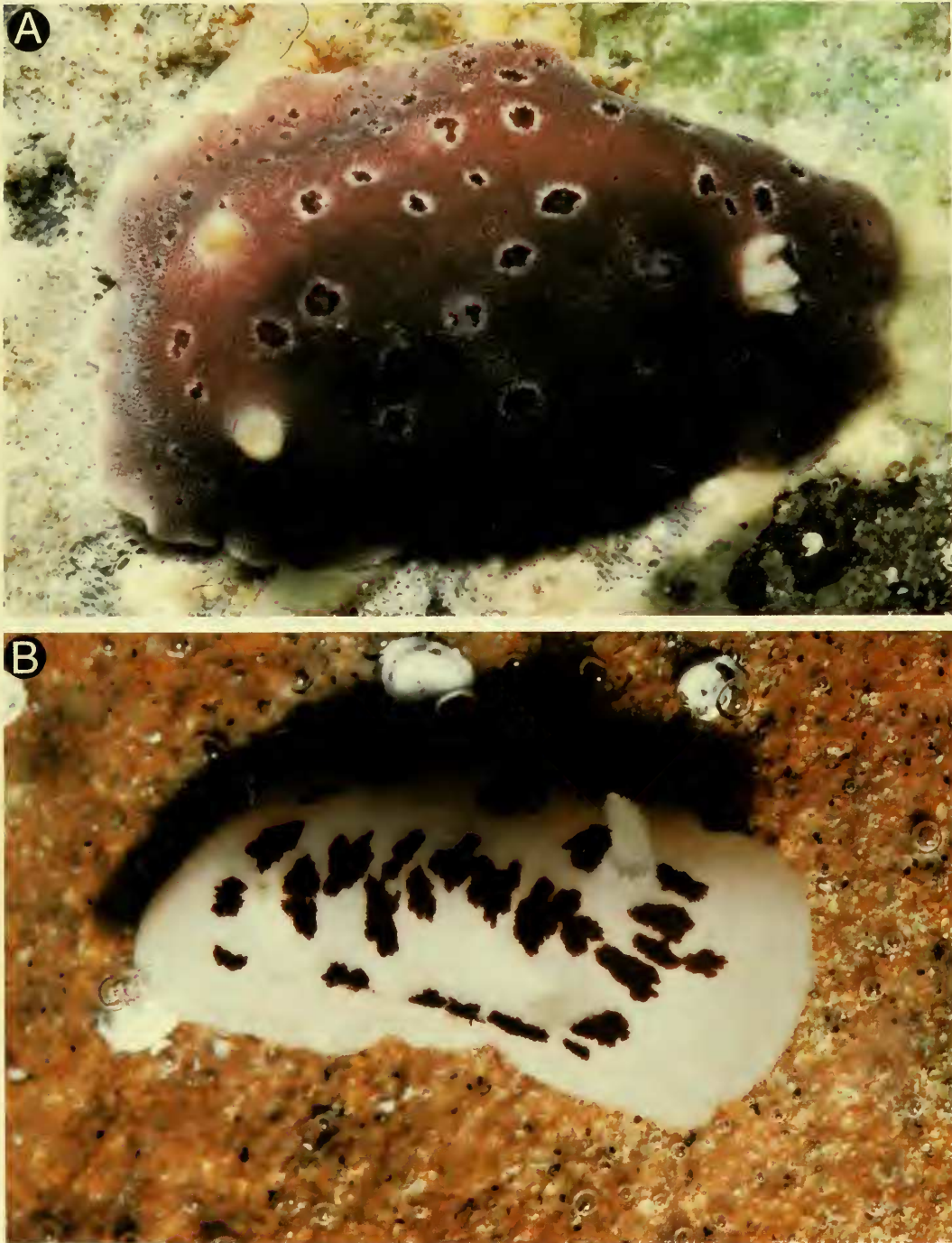


FIGURE 1. Living animals. A. *Gargamella gravastella* sp. nov, specimen from Dale Brook on the western shore of False Bay, South Africa, photograph by T. M. Gosliner. B. *Gargamella bovina*, sp. nov, specimen from Buffels Bay, on the False Bay coast of Cape Point, South Africa, photograph by T. M. Gosliner.

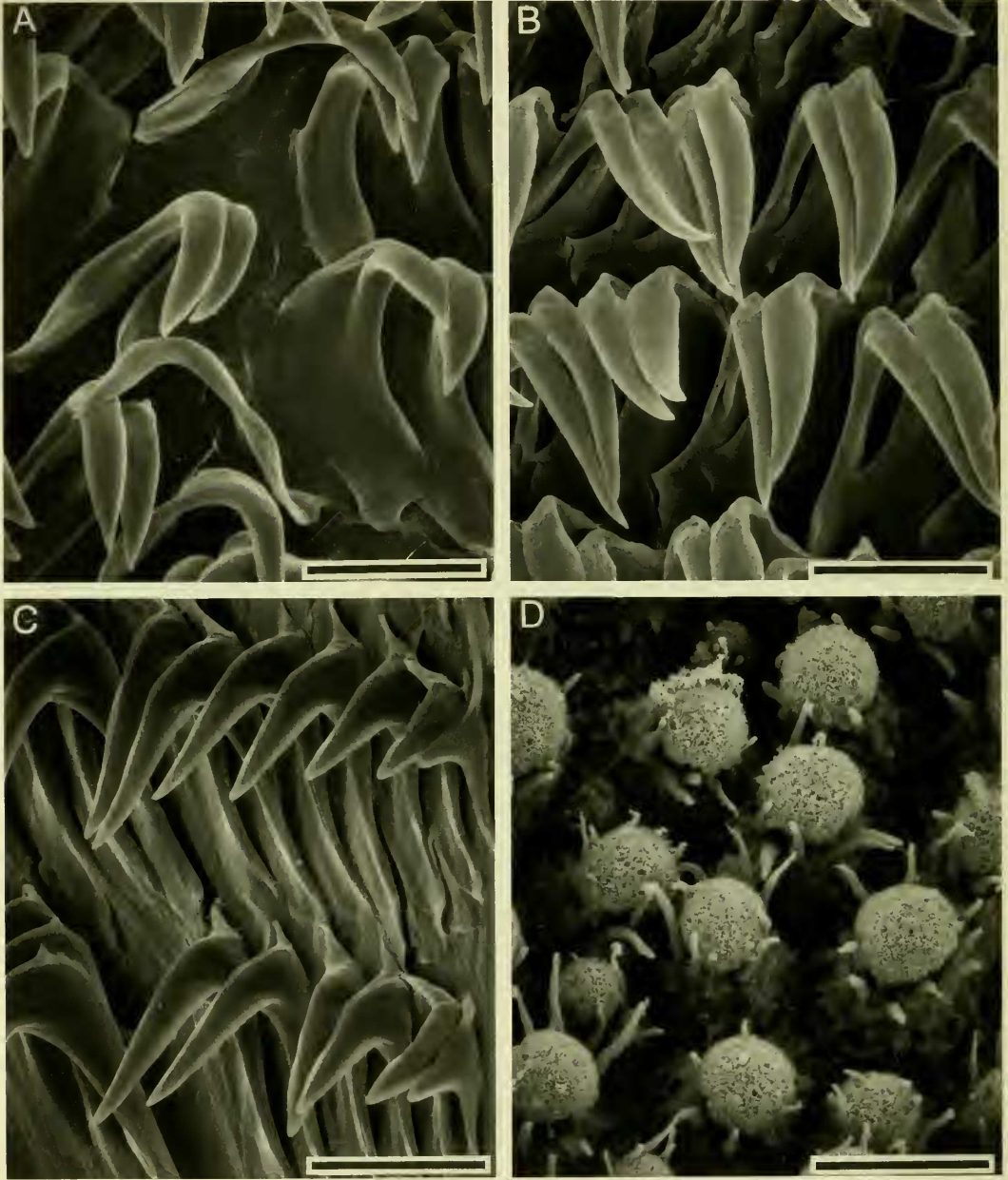


FIGURE 2. *Gargamella gravastella* sp. nov. (SAM A35383), scanning electron micrographs. A. Inner lateral teeth, scale = 43 μ m. B. Mid lateral teeth, scale = 60 μ m. C. Outer lateral teeth, scale = 43 μ m. D. Caryophyllidia tubercles, scale = 100 μ m.

long and convoluted. It joins the uterine duct. The uterine duct is short and enters the female gland mass at the base of the stalk of the small seminal receptacle.

REMARKS. — *Gargamella gravastella* is the only South African caryophyllidia-bearing dorid with a dark gray background color. Other distinctive features of this species are the dark gray spots, circled in white, that cover the notum. In fact, the coloration of *G. gravastella* distinguishes it from

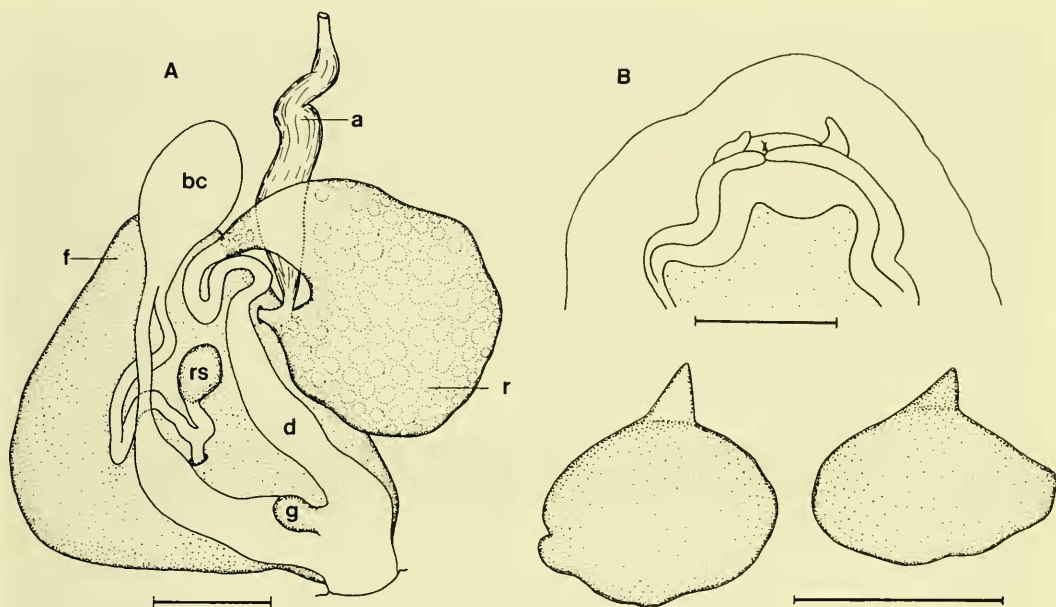


FIGURE 3. *Gargamella gravastella* sp. nov. (SAM A35381). A. Reproductive system, a = ampulla, bc = bursa copulatrix, d = deferent duct, f = female gland, g = accessory gland, p = prostate, rs = receptaculum seminis, scale bar = 0.5 mm. B. Ventral view of the anterior border of foot, scale bar = 1 mm. C. Penial hooks, scale bar = 0.1 mm.

G. immaculata, with colors ranging from solid white, to yellow or orange with darker rhinophores (Schrödl 1997). On the contrary, the pale yellow rhinophores of *G. gravastella* are much lighter than the rest of the body, with the exception of the matching pale branchial leaves.

As with *G. immaculata* (see Schrödl 1997), *G. gravastella* is densely covered with caryophyllidia tubercles, has penial hooks, a well-developed, large prostate, and an accessory gland. There are notable differences in the buccal armature of this species as compared to *G. immaculata*. Both the inner and mid lateral teeth of *G. gravastella* are wider and shorter than those of *G. immaculata*. Moreover, *G. gravastella* has fewer rows of teeth, 31–36 in two specimen, than does *G. immaculata*, which Schrödl (1997) reports as having from 60 to 91 rows.

The reproductive system of *G. gravastella* is also distinct. The overall shape of the bursa copulatrix is oval, rather than spherical, and the junction of the vaginal duct with the bursa copulatrix is directly adjacent to the duct connecting the bursa copulatrix with the receptaculum seminis, whereas the two ducts on the bursa copulatrix of *G. immaculata* are much farther apart (Marcus 1959; Schrödl 1997). The receptaculum seminis is notably smaller, and the accessory gland is smooth in contrast to the larger receptaculum seminis and lobate accessory gland of *G. immaculata*. Also, *G. gravastella* lacks the large vestibular hooks described in *G. immaculata* (Schrödl, 1997).

Gargamella bovina sp. nov.

Figs 1B, 4, 5

Gargamella sp. 2 Gosliner, 1987:71, fig. 95.

TYPE MATERIAL. — HOLOTYPE: off Danger Point, Cape Province, South Africa (34°32'34"S, 19°15'48"E), 44 m depth, 16 April 1984, 20 mm preserved length, collected by W. R. Liltved (SAM A36013). PARATYPES: off Danger Point, Cape Province, South Africa (34°32'34"S, 19°15'48"E), 44 m depth, 16 April 1984, one

specimen 20 mm preserved length, dissected, collected by W. R. Liltved (SAM A54296). Off Danger Point, Cape Province, South Africa (34°32'34"S, 19°15'48"E), 34 m depth, 11 April 1984, two specimens 16 mm preserved length, dissected, collected by W. R. Liltved (SAM A36010). Buffels Bay, False Bay, Cape Province, South Africa (34°19'03"S, 18°27'42"E), July 1982, one specimen 14 mm preserved length, dissected, collected by T. M. Gosliner (SAM A35385).

ETYMOLOGY. — *Gargamella bovina* is named for its external body coloration and pattern. The word *bovina* is Latin for "cowlike" and makes reference to the pattern of dark brown spots on the white notum that give this species an appearance similar to a Holstein dairy cow.

DISTRIBUTION. — Specimens of this species have been found off the coast of Cape Province, South Africa, off Danger Point and Buffels Bay as well.

EXTERNAL MORPHOLOGY. — The body is oval, with a slightly undulate mantle. It is white in color, with several dark brown irregular spots (Fig. 1B). The rhinophores and branchial leaves are also white. The perfoliate rhinophores consist of 14 transverse lamellae. The bipinnate gill consists of 7 branchial leaves. The anal papilla closes the circlet of branchial leaves. The notum of this animal is covered with many low caryophyllidia, measuring about 70 μ m. Each caryophyllidium bears a very small ciliated tubercle, and is surrounded by 5–7 short projecting spicules (Fig. 4D). The foot is broad with respect to the mantle margin. The anterior border of the foot is bilabiate and notched (Fig. 5B). The oral tentacles are well formed, and digitiform in shape.

BUCCAL ARMATURE. — The jaws are smooth, with no rodlets. The radular formulae of two specimens examined are $21 \times 38.0.38$ (SAM A36010) and $35 \times 40.0.40$ (SAM A35385). The inner lateral teeth are smooth (Fig. 4A), and gradually increase in size toward the mid-lateral teeth, which also lack denticles (Fig. 4B). The outer lateral teeth gradually decrease in size, the outermost lateral tooth being much smaller than the other outer lateral teeth (Fig. 4C).

REPRODUCTIVE SYSTEM. — The ampulla of this species is tubular, simple, and small (Fig. 5A). It branches and connects to a large, massive prostate and a short oviduct which connects to the female gland mass. The distal end of the prostate connects to an elongate, convoluted deferent duct. The distal end of the deferent duct is armed with four rows of penial hooks. The penial hooks have a broad base, 0.1 mm wide, and a long, straight hook, 37.5 μ m long (Fig. 5C). The vaginal duct is long, and narrower than the deferent duct. The proximal end of the vagina opens into the round bursa copulatrix. The duct connecting the bursa copulatrix and the sessile, spherical receptaculum seminis is long and narrow. This duct connects to the bursa copulatrix at a point far from, and nearly opposite the junction of the vaginal duct and bursa copulatrix (see Fig. 5A). The uterine duct is short and enters the female gland mass. A large, lobed accessory gland is present at the widened opening of the deferent duct and the vagina. The external surface of the gland bears a thin muscular connection to the female gland mass. This accessory gland does not contain any armature.

REMARKS. — *Gargamella bovina* is externally distinguishable from *G. gravastella* by its white background color, and dark brown spots. Its notal surface, though covered with caryophyllidia, has lower tubercles, very different from those of *G. gravastella*. Also, its coloration distinguishes it from *G. immaculata* which is solid white, yellow or orange (Schrödl 1997).

The buccal armature of *G. bovina* is different from *G. immaculata* in that there are fewer rows of teeth, 21–35 in two specimens of *G. bovina* compared with 60–91 rows in *G. immaculata* (Schrödl 1997). The smooth teeth of *G. bovina* and *G. immaculata* are similar in shape, but the teeth of *G. bovina* are considerably shorter than those of *G. immaculata*. The radula of *G. bovina* also differs from that of *G. gravastella* in the shape of the lateral teeth that are more elongate in the former.

The reproductive system of *G. bovina* closely resembles *G. immaculata*, more so than *G. gravastella*. Like *G. immaculata*, (see Marcus 1959; Schrödl 1997) the two ducts coming from the bursa copulatrix are situated far apart from each other. Also, the accessory gland is lobate in both *G. immaculata* and *G. bovina*. However, *G. bovina* bears a unique muscular attachment from the

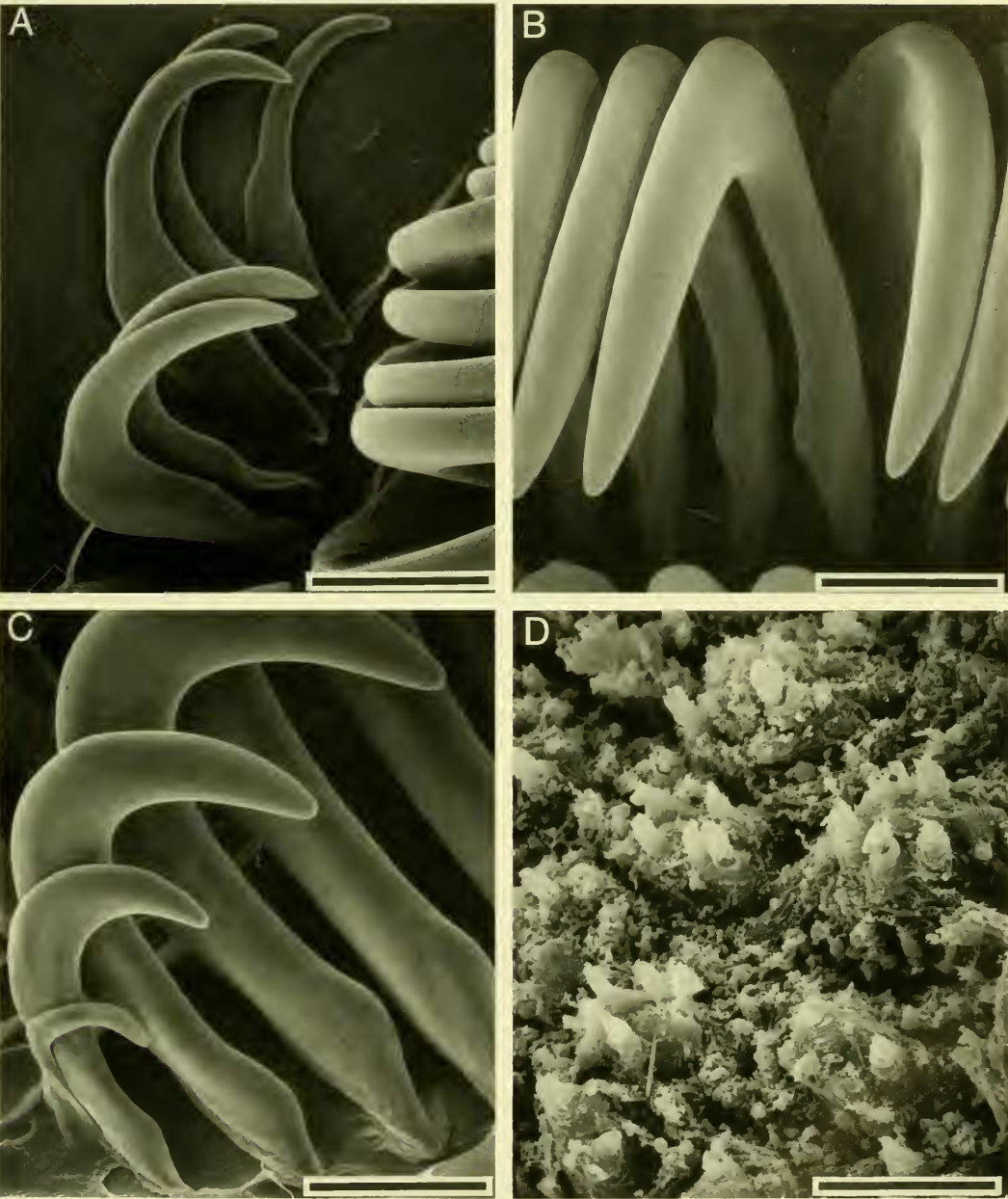


FIGURE 4. *Gargamella bovina* sp. nov., scanning electron micrographs. A. Inner lateral teeth (SAM A36010), scale = 60 μ m. B. Mid lateral teeth (SAM A36010), scale = 60 μ m. C. Outer lateral teeth (SAM A36010), scale = 43 μ m. D. Caryophyllidia tubercles, (SAM A36013) scale = 60 μ m.

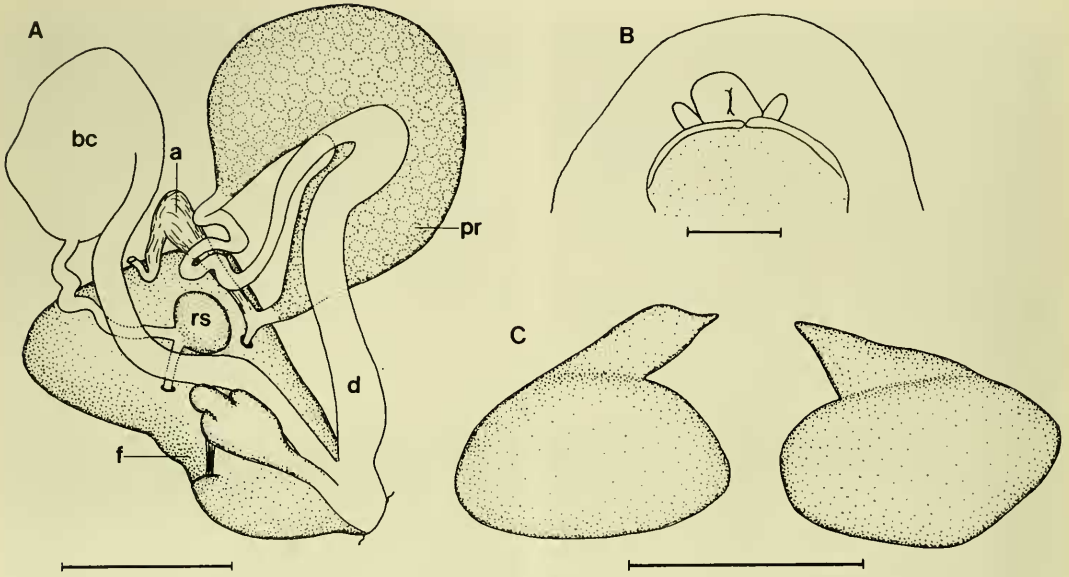


FIGURE 5. *Gargamella bovina* sp. nov. (SAM A36010). A. Reproductive system, a = ampulla, bc = bursa copulatrix, d = deferent duct, f = female gland, g = accessory gland, p = prostate, rs = receptaculum seminis, scale bar = 1 mm. B. Ventral view of anterior border of foot, (SAM A36013) scale bar = 1 mm. C. Penial hooks, scale bar = 0.1 mm.

accessory gland to the female gland mass. The receptaculum seminis is sessile, where that of *G. immaculata* is stalked. *Gargamella bovina* also possesses penial hooks, a feature common to this genus, but lacks the large vaginal hooks found in *G. immaculata*. The penial hooks of *G. bovina* have the same wide base as *G. gravastella*, but the cusp is notably longer.

DISCUSSION

The genus *Gargamella* was introduced by Bergh (1894) based on *Gargamella immaculata* Bergh, 1894, the type species by monotypy. He included the following features in the diagnosis of this genus: body somewhat depressed, dorsum silky, oral tentacles digitiform, branchial leaves tripinnate, anterior border of the foot notched and grooved, jaws and rachidian radular teeth absent, lateral teeth hook-shaped, prostate large, penis armed with hard spherical hooks, and vestibular gland present.

Ernest Marcus (1959) amplified the description of *G. immaculata* with anatomical information based on newly collected material. The most outstanding new feature described by Ernest Marcus is the presence of large copulatory spines in the atrium of *G. immaculata* and *Gargamella latior* Odhner, 1926, another nominal species described from South America. Schrödl (1997) redescribed *G. immaculata* and synonymized *G. latior* with it.

We have examined two specimens of *G. immaculata* collected from Seno Otway, near Punta Prat, Chile (SMNHI 12520) for comparison. We have found large hooks in the penis, but the vestibular hooks described by Ernest Marcus (1959) and Schrödl (1997) are actually situated in the opening of the vagina (Fig. 6A). The vestibular gland of this species opens in the atrium, and therefore we called it an accessory gland, to be distinguished from the vestibular glands of other dorids that open in a different position. The vaginal hooks are very large, with the base reaching up to 500 μm , and are arranged in a single row. The radula has hook-shaped, elongate teeth lacking denticles. The outermost lateral teeth are large, almost the same size as the innermost. Externally this species is characterized

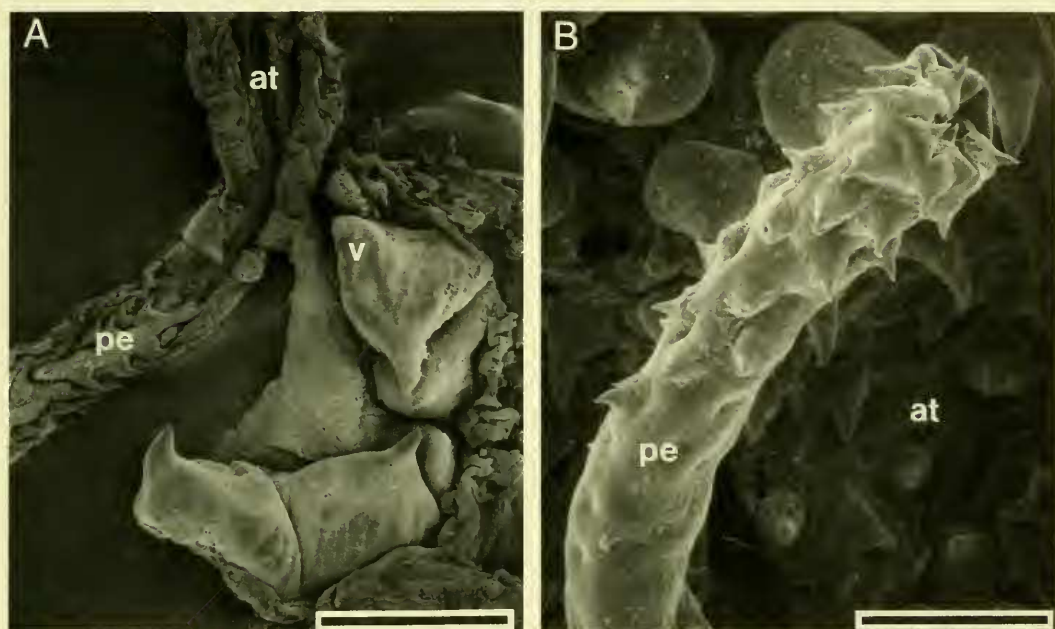


FIGURE 6. Scanning electron micrographs. A. Open atrium of *Gargamella immaculata* (SMNH 12520) showing the penial and vaginal hooks, at = atrium, pe = penis, v = vagina, scale bar = 750 μ m. B. Open atrium of *Baptodoris cinnabarina* (MNCN 15.05/32381) showing the penial and atrial hooks, at = atrium, pe = penis, scale bar = 150 μ m.

by a convex shape of the body, a wide foot and the presence of large caryophyllidia tubercles, about 200 μ m long.

Other genera probably related to *Gargamella* are *Baptodoris* Bergh, 1884 and *Platydoris* Bergh, 1877. In fact, Bouchet (1977) considered that *Gargamella* and *Baptodoris* were synonyms of *Platydoris*. The genus *Baptodoris*, type species *Baptodoris cinnabarina* 1884, is characterized by the presence of a large hooks in the atrium besides a penial papilla armed with an additional set of hooks (Fig. 6B), much smaller in size. It also has an accessory gland connected to the atrium. The lateral radular teeth of *Baptodoris* have one or more denticles, and the outermost laterals have many tiny denticles. Externally, *Baptodoris* is characterized by the presence of low caryophyllidia tubercles, a flattened body and a narrow foot. This pattern is consistent in the only two species of the genus that have been anatomically studied, *B. cinnabarina* and *B. mimetica* Gosliner, 1991. We have examined one specimen of *B. cinnabarina* collected from the Mediterranean coast of Spain (MNCN 15.05/32381), and information on *B. mimetica* was obtained from Gosliner (1991). Other species assigned to this genus are not sufficiently described to verify the presence of these characteristics.

The genus *Platydoris*, type species *Platydoris argo* Linnaeus, 1758, includes large species with a ventrolaterally flattened body and a narrow foot. An anatomical study of *P. argo* based on specimens collected from Northern Spain (CASIZ 115217), revealed the presence of several rows of large hooks in the vagina and smaller hooks in the penis, about 50 μ m long, much smaller than those of *G. immaculata*. A large accessory gland opens in the atrium. In addition, the prostate of *Platydoris* is very small, the caryophyllidia tubercles are very low, and the outer lateral radular teeth are very small. Other species of *Platydoris*, such as *Platydoris formosa* (Alder and Hancock 1866), may lack vaginal hooks (see Kay and Young 1969), but this point needs confirmation.

Gargamella gravastella and *G. bovina* appear to be more closely related to *G. immaculata* than to *P. argo* or *B. cinnabarina*. The species from South Africa differ from *G. immaculata* in lacking

vaginal hooks. However, the morphology of the penial hooks is very similar in these three species. In all three the penial hooks have a broad base, 0.1 mm wide, and a long, straight cusp. *G. immaculata*, *G. gravastella*, and *G. bovina* all have a large prostate and an accessory gland that opens in the atrium. They also share similar radular morphology, with large, smooth marginal teeth, and mid-lateral teeth with elongated cusps also lacking denticles. The caryophyllidia tubercles are also well-formed in these three species.

PHYLOGENETIC ANALYSIS

In order to determine the phylogenetic relationships of *Platydoris*, *Gargamella* and *Baptodoris*, and therefore the systematic position of the two new species from South Africa, we have carried out a phylogenetic analysis. For this analysis, we have included the two new species from South Africa described in this paper, as well as *Gargamella immaculata*, *Baptodoris cinnabarina*, *Baptodoris mimetica*, *Platydoris argo*, *Platydoris angustipes* (Mörch, 1863), *Platydoris stomascuta* Bouchet, 1977 and *Platydoris maculata* Bouchet, 1977. Information regarding *G. immaculata*, *B. cinnabarina* and *P. argo* was obtained from our own anatomical studies. Data on *P. angustipes* was extracted from Ernest Marcus (1957), data on *P. stomascuta* and *P. maculata* from Bouchet (1977) and data on *B. mimetica* from Gosliner (1991).

To polarize the morphological variability we have selected *Diaulula sandiegensis* (Cooper, 1862) as the outgroup. Information on this species has been obtained from our own dissections of one specimen collected from California (CASIZ 068277).

The following characters (Table 1) were considered in undertaking the phylogenetic analysis:

1. Body shape. Species of *Baptodoris* and *Gargamella*, including the two new species from South Africa have a convex body. On the contrary, species of *Platydoris* have a flattened body. A convex body is also present in *D. sandiegensis* and it is regarded as the plesiomorphic condition.

2. Foot width. Species of *Platydoris* and *Baptodoris* have a narrow foot, whereas *Diaulula* and *Gargamella*, including *G. bovina* and *G. gravastella*, have a wide foot. A narrow foot appears to be apomorphic.

3. Branchial sheath. In *Platydoris argo* and *P. maculata* the branchial sheath is lobate, whereas in the other species of *Platydoris*, *Gargamella*, *Baptodoris* and *Diaulula* it is rounded. A lobate branchial sheath is considered apomorphic.

4. Caryophyllidia. In species of *Platydoris* and *Baptodoris*, the caryophyllidia are very low and difficult to recognize with an optical microscope. In *Gargamella*, including the species from South Africa and *Diaulula*, the caryophyllidia are large and conspicuous. Small caryophyllidia are considered apomorphic.

5. Lateral radular cusp. The cusps of the radular teeth of *G. immaculata*, *G. bovina* and *G. gravastella* are very elongate, longer than the base of the teeth. In *Platydoris*, *Baptodoris*, and *Diaulula* the cusps are always shorter than the base of the teeth. An elongate radular cusp is considered apomorphic.

6. Lateral radular teeth denticles. In species of *Baptodoris* the lateral radular teeth have one or more denticles that are absent in *Diaulula*, *Platydoris* and *Gargamella*. The presence of denticles on the lateral radular teeth is considered apomorphic.

7. Outermost radular cusp. The outermost lateral teeth of *Platydoris* and *Baptodoris* are short plates (there is no information on *P. stomascuta* and *P. maculata*), whereas in *Gargamella* and *Diaulula* they are typical hamate teeth similar in shape to the other radular teeth. The presence of hamate outermost lateral teeth is regarded as plesiomorphic.

8. Outermost lateral teeth denticles. In *Baptodoris*, the outermost lateral teeth have a number of tiny denticles that are not present in *Platydoris*, *Gargamella* and *Diaulula*. The presence of these denticles is considered the apomorphic condition.

TABLE 1. Character states for the taxa involved in the phylogenetic analysis. Data code: 0 = plesiomorphic condition; 1, 2 = apomorphic condition; ? = missing data.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>D. sandiegensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	?	0
<i>P. argo</i>	1	1	1	1	0	0	1	0	1	1	0	1	1	1
<i>P. angustipes</i>	1	1	1	1	0	0	1	0	1	1	0	1	1	1
<i>P. maculata</i>	1	1	0	1	0	0	?	0	0	1	0	1	0	1
<i>P. stomascuta</i>	1	1	0	1	0	0	?	0	0	1	0	1	0	1
<i>G. immaculata</i>	0	0	0	0	1	0	0	0	0	2	1	1	0	1
<i>G. bovina</i>	0	0	0	0	1	0	0	0	0	2	1	0	?	1
<i>G. gravastella</i>	0	0	0	0	1	0	0	0	0	2	0	0	?	1
<i>B. cinabarina</i>	0	1	0	1	0	1	1	1	0	1	1	1	0	1
<i>B. mimetica</i>	0	1	0	1	0	1	1	1	0	1	0	1	0	1

9. Prostate size. The prostate of *P. argo* and *P. angustipes* is very small compared to those of *P. stomascuta*, *P. maculata*, *Baptodoris*, *Gargamella* and *Diaulula*. Presence of a small prostate is considered apomorphic.

10. Penial hooks. In *Diaulula* there are no penial hooks. In species of *Platydoris* and *Baptodoris* the hooks are small, never larger than 70 µm, whereas in *Gargamella* the penial hooks are very large, over 120 µm long. Absence of penial hooks is considered plesiomorphic. This character is treated as unordered in the analysis.

11. Bursa copulatrix ducts. Two ducts lead from the bursa copulatrix of all species included in the analysis. In species of *Platydoris*, *G. gravastella*, *B. mimetica* and *D. sandiegensis* these ducts are immediately adjacent to each other. In the remaining species of *Gargamella* and *B. cinabarina*, there is some distance between the two ducts. Having the ducts separated by some distance is considered apomorphic.

12. Vaginal and atrial hooks. In *Baptodoris*, *Platydoris* and *G. immaculata* there are very large hooks situated in the atrium and in the opening of the vagina. These hooks are absent in *Diaulula*, *G. bovina* and *G. gravastella*. The absence of vaginal or atrial hooks is considered plesiomorphic.

13. Vaginal hooks position. In *G. immaculata*, *P. maculata*, *P. stomascuta* and *Baptodoris*, the atrial hooks are situated in the atrium or in the opening of the vagina, whereas in *P. argo* and *P. angustipes* the hooks are situated along the vaginal duct. The latter position is considered apomorphic.

14. Accessory gland. In *Baptodoris*, *Platydoris* and *Gargamella* there is a lobate accessory gland that opens in the atrium. This gland is absent in *Diaulula*. The absence of the atrial glands is considered the plesiomorphic condition.

In order to develop phylogenetic hypotheses regarding these taxa, the above described characters were placed in a data matrix (Table 1) and analyzed by means of Phylogenetic Analysis Using Parsimony (PAUP), version 3.1.1, using the exhaustive algorithm. A single most parsimonious tree was obtained (Fig. 7). This tree requires 17 steps, has a consistency index of 0.88 and a retention index of 0.92.

The tree obtained clearly supports the placement of *G. bovina* and *G. gravastella* in the genus *Gargamella*, which is the sister group of the clade formed by *Platydoris* and *Baptodoris*. It is also evident from this phylogenetic hypothesis that *Platydoris* and *Baptodoris* form a monophyletic group, supported by 3 synapomorphies: narrow foot (2), small caryophyllidia tubercles (4), and plate-shaped, outermost radular teeth (7). Within the genus *Gargamella*, which is supported by a single synapomorphy, radular teeth with elongate cusps (5), *G. gravastella* is the sister group of the other two species. *Platydoris* is also supported by a single synapomorphy, flattened body (1). *Baptodoris* is the sister

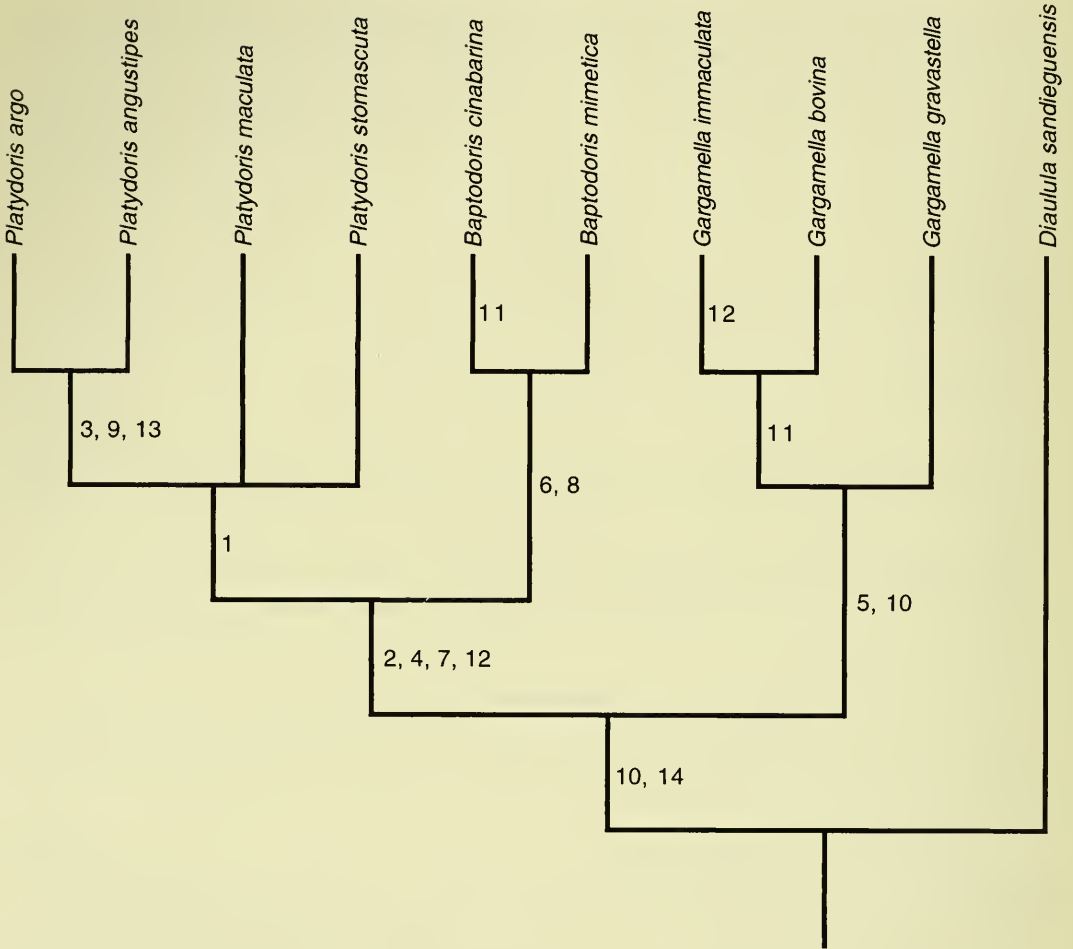


FIGURE 7. Hypothesis of phylogeny of *Gargamella*, *Platydoris* and *Baptodoris*. Numbers refer to characters listed within the text.

group of *Platydoris* and it is supported by two synapomorphies, lateral teeth denticulate (6) and outermost lateral teeth with minute denticles (8). *Platydoris maculata* and *P. stomascuta* appear to be members of the genus *Platydoris*, but there is not enough resolution to determine their relationships with *P. argo* and *P. angustipes*.

BIOGEOGRAPHY

The genus *Gargamella* now includes three valid described species. *Gargamella immaculata*, the type species, was described from Argentina and is also known from Chile (Schrödl 1997). With the description of *Gargamella gravastella* and *Gargamella bovina* from South Africa, it is apparent that members of this genus are restricted to southern oceans.

It is evident that the highly developed penial armature of *G. immaculata* is more derived than that of the two South African species (see Phylogenetic Analysis), perhaps indicating a more recent divergence from their common ancestor. Preliminary phylogenetic analysis of outgroups of *Gar-*

gamella indicates that they are more closely related to species of *Platydoris* and *Baptodoris* than to any other caryophyllidia-bearing dorids. Species of *Platydoris* are found throughout tropical and subtropical waters, with no cold water southern ocean representatives. The genus *Baptodoris* is also absent in the southern ocean cold waters. Only one representative was described from the South Pacific, *Baptodoris fongosa* Risbec, 1928 from the warm waters of New Caledonia. However, this species was poorly described and its generic placement is uncertain.

These facts suggest that the southern distribution of *Gargamella* today is not a result of ancient Gondwanan distributions, but is more likely a result of more recent vicariant and distributional events. This is also a more likely scenario, owing to the fact that members of these genera are among the more highly derived cryptobranch dorids.

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